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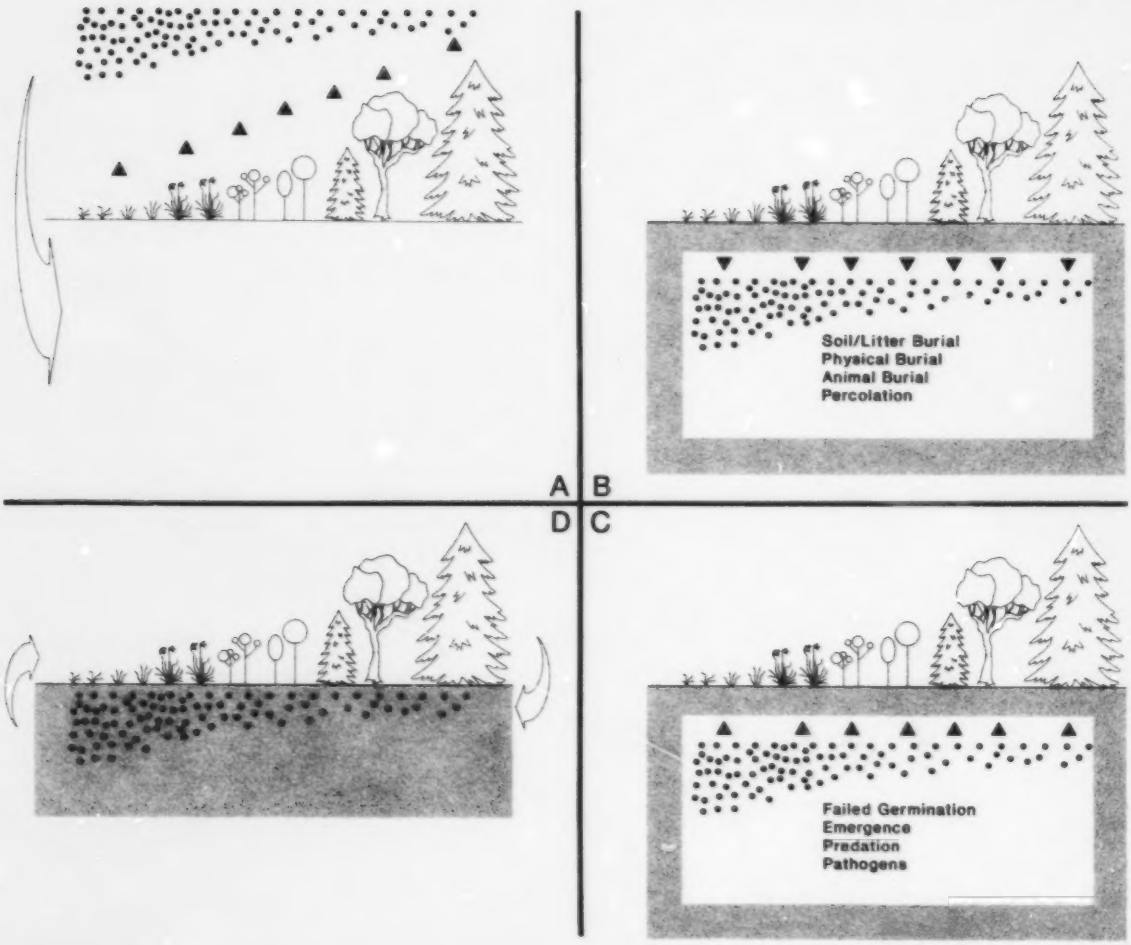
The Function of Seed Banks in Northern Forest Ecosystems

(A Literature Review)



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Cover Illustration

Soil seed bank dynamics, a continuum:

A: Seed rain.
B: Seed incorporation into the soil seed bank.
C: Seed loss from the soil seed bank.
D: Seed bank size and diversity during succession.

The Function of Seed Banks in Northern Forest Ecosystems

(A Literature Review)

by
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ABSTRACT

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The phenomenon of seeds remaining dormant within the soil is well known and documented. Detailed information on the role of such "seed banks" in northern Ontario, however, is extremely limited. Research is required to determine the species and abundance of seeds in the soil across a range of forest types, as well as to determine the function of the seed bank in post-disturbance vegetation dynamics. Comparison tables of seed density and diversity are presented for the boreal and deciduous forest types and the research that has been conducted is discussed. This review includes detailed discussions of: (1) seed bank dynamics, (2) physiology of seeds in a seed bank, (3) boreal and deciduous forest seed banks, (4) seed bank dynamics and succession, and (5) recommendations for initiating a seed bank study in northern Ontario. Understanding the seed bank and its related processes will increase our knowledge of post-disturbance vegetation patterns and allow for more accurate predictions of the response of natural vegetation following a disturbance. In addition, an improved decision-making process for the recolonization of sites, vegetation management, and vegetation control will result.

Keywords: boreal forest, deciduous forest, seed banks, seed enumeration, seed germination, seed dormancy, seed input, seed losses

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1.0 OVERVIEW OF SEED BANKS

1.1 INTRODUCTION

Seed dormancy within the soil has been documented in the scientific literature for more than a century. Seed banks were first recognized by farmers, who found more weeds sprouting after working and weeding their fields. Most of the information on soil seed banks originates from either agricultural research or research from other intensively managed ecosystems in which the contents of the soil seed bank may pose a threat to the crop species.

All viable seed present under and on the surface of the soil or associated with the soil litter constitutes the "soil seed bank" (Leck *et al.* 1989). Each soil seed bank has spatial and temporal dimensions and displays both vertical and horizontal dispersion that reflect seed dispersal mechanisms and subsequent movement of the seed through the soil. If conditions are favourable after a disturbance, some seed within a seed bank will break dormancy and germinate. Seeds are usually most abundant near the soil surface and their numbers decline rapidly with depth. Rainwater tends to wash small seeds deeper into the soil than large seeds and some are buried by the activity of worms and others animals. Seeds are lost from the seed bank through germination, predation and decay.

Seed that remains in the cones or fruit of the tree constitutes another type of seed bank the "canopy seed bank". Seed is held in the canopy until conditions warrant dispersion, especially in the case of serotinous and semi-serotinous tree species. For the purposes of this report, the term seed bank will refer to the soil seed bank unless stated otherwise.

The intent of this report is to detail the processes within forest seed banks in order to determine where gaps in our knowledge exist. With this information, a soil seed bank study can be designed and initiated in northern Ontario to obtain a quantitative description of the seed bank across a range of vegetation types at various developmental stages. Much of the effort should be concentrated on the role of seeds in the soil for post-disturbance vegetation dynamics following both natural and anthropogenic disturbance.

1.2 HISTORY OF SEED BANK RESEARCH

Early agriculturists were aware of the presence of seeds in the soil. They knew that this seed reservoir had the potential to germinate and become incorporated into the crop (Baker 1989). Banks of weed seeds have been studied longer and more intensively in agriculture than other types because of the threat to agricultural crops. The earliest research was conducted by biologists studying weed biology (Brenchley 1918; Chippendale and Milton 1934; Champness and Morris 1948). The focus of early research was seed viability, since this is crucial to the success of germination from within the seed bank. Early experiments conducted by Beal (1879) and Duvel (1905) studied seeds that were buried and then exhumed at regular intervals. In Beal's experiment three species *Verbascum blattaria*, *V. thapsus* and *Malva rotundifolia* remained viable after 100 years (Kivilaan and Bandurski 1981). Toole

and Brown (1946) found that almost 25% of the seed remained viable in Duvel's experiment after 40 years. Both of these early researchers recognized that the major limitation of their studies was breaking the dormancy of the buried seed. More recent work on dormancy, germination, and general seed physiology has been conducted by Bewley and Black (1982), Baskin and Baskin (1978, 1984, 1987, 1989, 1990) and Buchele *et al.* (1991a,b). These studies identified characteristics that regulate the germination and dormancy of seed, thus allowing better estimates of seed bank populations and provides a basis against which to interpret the results.

Seed banks are found wherever soil and seeds coexist. Seed banks have been studied in numerous terrestrial ecosystems including coniferous, deciduous and tropical forests, arctic and alpine communities, deserts, wetlands, wastelands, grasslands, pastures, and meadows.

1.3 CLASSIFICATION OF SOIL SEED BANKS

Seed banks can generally be divided into two distinct classifications, "transient" and "persistent" seed banks. Seed in a transient seed bank remains viable for less than 1 year, whereas seed in a persistent seed bank can remain viable for a much longer period. A number of generalizations on seed viability and longevity have been proposed and are outlined by Harper (1977). These include: (1) long-lived seeds are characteristic of disturbed habitats, (2) long-lived seeds are usually from annual or biennial plants, (3) seeds that remain viable for long periods of time are generally small, and (4) aquatic plants have long-lived seeds because conditions in mud may inhibit decay. Thompson and Grime (1979) found that plant and tree species have a wide range of seed bank types, based primarily on the survival strategy of the species. The seeds in a transient seed bank are not usually buried in the soil, whereas the majority of seeds in a persistent seed bank are. Houle and Payette (1990, 1991) determined that some deciduous forest types are characterized by transient winter seed banks. This supports the conclusions of Thompson and Grime (1979) and Grime (1981), who indicate that seeding period (time and duration), germination, and dormancy play important roles in determining the classification of a seed bank (persistent or transient). Thompson and Grime (1979) further divided the two general classifications of seed banks (transient and persistent) into four main types (Fig. 1). Types I and II are transient; types III and IV are persistent. From Figure 1, it is possible to recognize some physiological and morphological characteristics of seeds associated with each type of seed bank. Considerations of the mechanisms of seed physiology and morphology in relation to viability and the timing of germination are important because they help determine the success of seedling establishment.

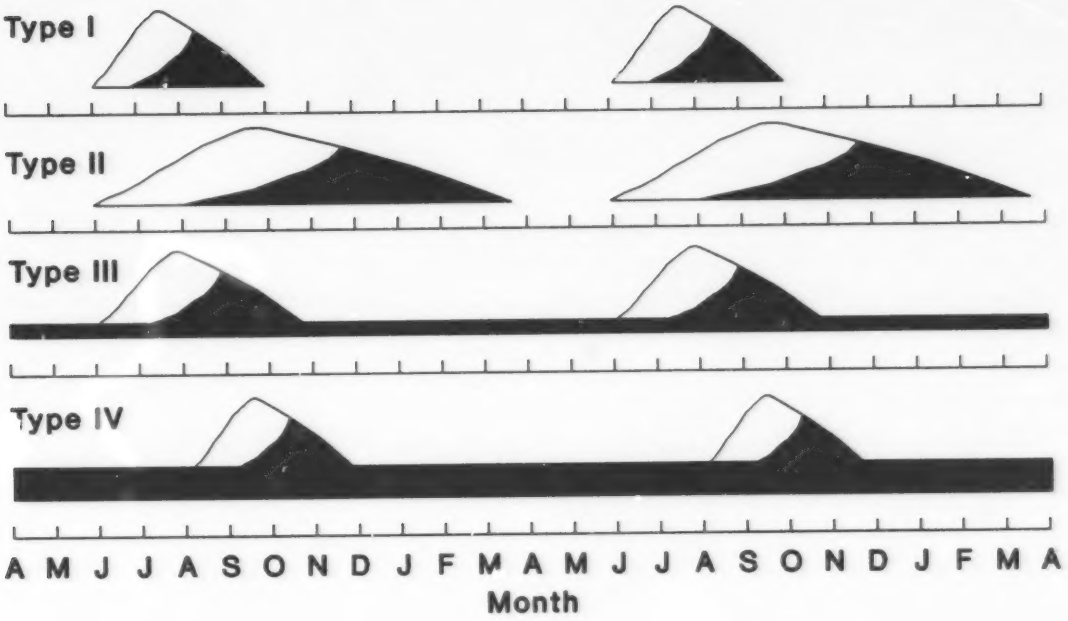

Figure 1. Diagrammatic representation of the four types of seed banks (from Thompson and Grime 1979). Shaded areas represent seeds capable of germinating immediately after removal to suitable growing conditions. Unshaded areas represent viable seeds that are incapable of immediate germination. **Type I**: annual and perennial grasses of dry or disturbed areas. **Type II**: annual and perennial herbs colonizing vegetation gaps in early spring. **Type III**: species that mainly germinate in the autumn but which maintain a small persistent, seed bank. **Type IV**: annual and perennial herbs and shrubs with a large persistent seed bank.

1.4 DYNAMICS IN A FOREST SEED BANK

Seed banks play a crucial role in the dynamics of plant populations. For example, after a disturbance such as harvesting, fire, or windstorm, newly created openings or gaps in a forest stand become repopulated by plants that arise primarily from vegetative propagation, a seedling bank, seed rain or a seed bank (Kellman 1974). Seed banks function as a source of continuous propagules to ensure the continual occupation of a site (Grime 1981). In addition, they can serve as a gene pool by buffering a plant population from local extinction and preserving the population of a species within a community (Kalisz 1991; Roberts 1991). The relative importance of seed recruitment from the seed bank differs among plant species and among plant communities (Harper 1977; Fenner 1985). The dynamics of a seed bank include recruitment into the dormant seed bank population *via* seed rain (any seed input into soil) and

losses to the dormant seed bank through seed predation, death, or transferral into the active seed bank *via* a stimulus (usually a disturbance to the existing vegetation). Figure 2 illustrates the complexities of a soil seed bank in relation to vegetation dynamics.

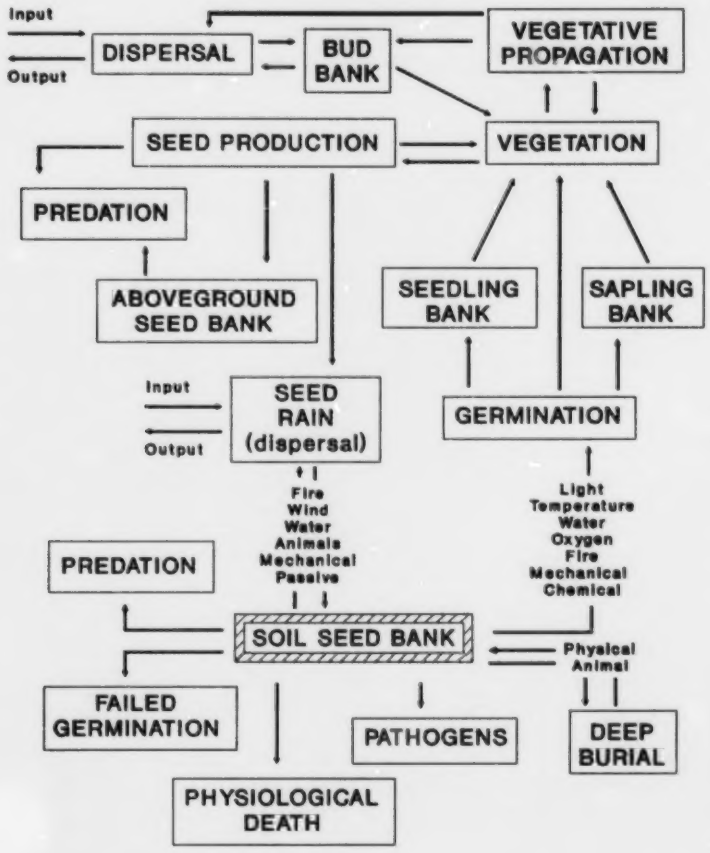

Figure 2. Model of seed bank and vegetation dynamics (from Simpson *et al.* 1989).

Seed bank dynamics depend upon many factors, including: (1) seed sources (species and abundance), (2) seed dispersal (annual seed fall), (3) seed predation, (4) seed decay, and (5) soil type and conditions. The major factors that cause seed loss in a seed bank are consumption by predators, decomposition and decay, and *in situ* germination (Harper 1977). Seed longevity has been found to be heritable (Harper 1977).

2.0 FOREST SEED BANK PROCESSES

There are many processes that regulate seed banks, including seed bank losses from predation, disease, germination, and the physiological state of the seed in relation to dormancy and germination.

2.1 ECOPHYSIOLOGY OF SEED IN A SEED BANK

Seed ecophysiology covers all aspects of seed physiology and morphology (Baskin and Baskin 1990). Ecophysiological considerations for seed include germination, germination requirements, dormancy, and dormancy requirements, all of which are important factors that influence the successful germination and establishment of a seedling.

2.1.1 Germination

Germination is the resumption of growth by the embryonic plant, which has remained dormant in the seed. Germination occurs when the seed begins to imbibe moisture. The establishment of a germinated seed is almost exclusively dependent upon favourable environmental conditions including light, moisture, and temperature.

Each species has its own set of germination requirements. The response of seeds to a great variety of environmental conditions can be regarded as an adaptation for maximizing the likelihood of surviving in an unpredictable environment (Fenner 1985). There is a complex interaction among the pre- and post-germination conditions required for successful seed germination and seedling establishment. Factors involved in this complex interaction include environmental, physiological, and morphological conditions.

2.1.2 Dormancy

Seed dormancy refers to the delaying mechanism that prevents germination under conditions that are unfavourable for establishment (Fenner 1985). Alleviation of dormancy is required for germination to occur, but does not itself stimulate germination; it is, however, a necessary prerequisite (Fenner 1985). Dormancy can be divided into at least three categories: primary, relative, and secondary (Bewley and Black 1982). Unfortunately, there are a number of different terminologies employed, which results in some confusion. For the purposes of seed bank dormancy, the terminology of Baskin and Baskin (1989) will be followed. Baskin and Baskin (1989) list five types of dormancy exhibited by mature seed in a seed bank (Table 2.1). These types are: (1) physiological, (2) physical, (3) combinational, (4) morphological, and (5) morpho-physiological.

Most species with seeds in the soil seed bank have a physiological type of dormancy. For each of the types of dormancy described by Baskin and Baskin (1989) in Table 2.1 there are three states of dormancy that form a dormancy continuum (Baskin and Baskin 1985). These states of dormancy are: (1) dormant (more aptly referred to as innately dormant), in

which seeds will not germinate under any set of normal environmental conditions (2) conditionally dormant, an intermediary stage in which seeds will germinate only under a limited range of environmental conditions and (3) nondormant, where seeds will germinate over the widest range of conditions possible. Thus, there exists a gradient or continuum of changes in germination responses as seeds pass from dormancy through a conditionally dormant state to nondormancy. Fluctuations in light, moisture, and temperature all contribute to meeting the dormancy requirements of a seed so that successful germination can take place. Before germination occurs, these same treatments (light, moisture and temperature) can also initiate the breaking of dormancy. It has been found that certain annual species go through an annual dormancy cycle, periods of decreased and increased dormancy (Baskin and Baskin 1985; Harrison 1991; Reisman-Berman *et al.* 1991).

Table 2.1. Types, causes and characteristics of seed dormancy (Baskin and Baskin 1989).

Dormancy	Cause(s) of dormancy	Embryo
Physiological	Physiological inhibiting mechanism of germination in the embryo	Fully developed; dormant
Physical	Seed coat impermeable to water	Fully developed; nondormant
Combinational	Impermeable seed coat; physiological inhibiting mechanism of germination in the embryo	Fully developed; dormant
Morphological	Underdeveloped embryo	Underdeveloped; nondormant
Morpho-physiological	Underdeveloped embryo; physiological inhibiting mechanism of germination in the embryo	Underdeveloped; dormant

2.1.3 Germination of buried seeds

Each of the five types of dormancy listed in Table 2.1 has specific requirements that must be met before germination can occur (Table 2.2). The information in Table 2.2 was compiled from a number of reports (Baskin and Baskin 1978, 1984, 1985, 1987, 1989, 1990; Fenner 1985; Priestley 1986; Reisman-Berman *et al.* 1991).

Baskin and Baskin (1989) state that most species which rely on seed banks for perpetuation and survival have some degree of physiological seed dormancy and many display annual cycles in germination requirements due, in part, to fluctuating temperatures. The

primary reason that seeds do not germinate is that each species has a specific set of germination requirements that are seldom met. As a result, many estimates of seed bank populations and diversity are too low (Baskin and Baskin 1989).

Table 2.2. Requirements for breaking dormancy, seed viability and seed bank classification for five types of dormancy.

Dormancy	Requirements for breaking dormancy[1]	Seed viability	Classification of seed bank
Physiological	cyclical dormancy; after-ripening; high temperature (spring and summer); light; moisture; disturbance	<1 year	transient
Physical	cyclical dormancy; fluctuating temperatures (renders seed coat permeable); light; moisture; favourable position in soil profile at proper time of year	varies	persistent
Combinational	fluctuating temperatures (renders seed coat permeable); either high summer or low winter temperatures; moisture	>100 years	persistent
Morphological	complete embryo development; light	<1 year	transient
Morpho-physiological	complete embryo development; after-ripening; high summer and low winter temperatures	up to 3 years	persistent

[1] Each species has its own characteristic set of germination requirements that need to be met for germination to proceed.

Appendix A contains a list of species common to northwestern Ontario that have been known to rely to some extent on seed banks as a mode of reproduction. Appendix A also includes seed dispersal information. Appendix B contains information on germination and stratification requirements for these common seed bank species in northwestern Ontario. The information in Appendix B was compiled from a number of sources including Bell (1991), Walsh and Krishka (1991), Sims *et al.* (1990) and Schopmeyer (1974).

2.2 PREDATION IN SEED BANKS

Predation of seeds in the seed bank by birds, small mammals, rodents and a variety of insects can lead to significant losses (Harper 1977; Louda 1983, 1989; Hendrix 1988). Louda (1989) suggests some generalizations that can be made about seed predation, as follows: (1) seed predators help create the difference between transient and persistent seed banks, (2) predation in the seed bank is dependent upon the location within the potential environmental range of the predator, (3) species that depend upon seed for recolonization are particularly vulnerable to predation, and (4) all predators that feed on the seed before and after germination can influence the number of seeds in the seed bank.

Larger seeds are generally more vulnerable to predation (Louda and Zedler 1985), leading to the conclusion that species with large seeds tend to form transient seed banks whereas small-seeded species form persistent seed banks (Hendrix 1988). The predatory activities of mammals, rodents, birds, and insects significantly affect the species composition of seeds in the seed bank as well as seed distribution within the soil profile and across a habitat. Predators change seed distribution by eating, moving or caching seed. Recently, Reader (1991) suggested that the removal of ground cover (plant biomass and litter) can reduce seed predation. This relationship hypothesizes that the ground cover provides a habitat for seed predators, and thereby increases seed predation.

2.3 OTHER LOSSES FROM THE SEED BANK

Several factors other than predation lead to seed loss, including: decomposition, decay, *in situ* germination, and loss of seed vigour as a result of physiological ageing (Harper 1977; Fenner 1985; Priestley 1986; Louda 1989). Decay seems to cause the greatest seed loss (Harper 1977). Seed rotting is affected by both the temperature and moisture status of the soil, indicating that the physical conditions of the environment can determine the probability of seed survival (Sarukhan 1974).

Seed burial experiments indicate that an exponential depletion rate is possible for some species. Depletion rates appear to increase with increased disturbances. Seed buried at shallow depths have a higher depletion rate than seeds buried deeper in the soil profile (Sarukhan 1974; Granström 1986, 1987). Cardina *et al.* (1991) found a decrease in species diversity in the seed bank with increasing soil disturbance. Conn and Farris (1987) reported that burial depth had a significant effect on seed longevity for some species. Soil properties such as clay content, pH, and the abundance of certain chemical elements (P, K, Mg, and Mn) had an effect on the occurrence of some weed species (Andreasen *et al.* 1991).

3.0 SEED BANKS AND VEGETATION TYPES

3.1 BOREAL FOREST SEED BANKS

The boreal forest is typified by large tracts of mixedwood species including white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill] B.S.P.), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) (Rowe 1972). It stretches across most of North America and is generally characterized by long, cold winters and short, warm summers. The soil seed bank has been extensively studied across a range of boreal forest conditions, stand types, and climatic regions (Frank and Safford 1970; Silc and Haavisto 1970; Kellman 1970, 1974; Ahlgren 1979a,b,c; Hill and Stephens 1981; Isaac 1982; Vermeer 1984; Collins 1985; Kramer and Johnson 1987; Morgan and Neuenschwander 1988).

The seed bank represents a mechanism of survival for species growing in the boreal forest and subject to periodic disturbance (Archibold 1989). Disturbances can be characterized in three ways: (1) time that has passed since the last disturbance, (2) size of the disturbance, and (3) the intensity of the disturbance (Granström 1986). Fire has been the main natural disturbance in the past, and therefore, the size of the seed bank reflects the type, intensity, and frequency of the fire (Archibold 1989). Burned areas tend to release more seed from the seed bank than unburned areas (Ahlgren 1979b,c). The other major disturbances to the boreal forest include harvesting, windthrow, insect defoliation, and loss of timber to disease.

Seed banks in the boreal forest can have a high density of seed, but the seeds often are not viable or lose viability quickly. The results of Frank and Safford (1970) indicate that seed banks of the coniferous forest in Maine have transient seed banks and that seed from the soil should not be relied upon for natural regeneration. Similar results were found for black spruce in the boreal forest (Fraser 1976). Granström (1986) supports this hypothesis and reports that successful establishment from seed banks seems to be rather uncommon in some forest types.

Ahlgren (1979a,b,c) found that the amount of seed in the seed bank varied with the time since the disturbance (fire or harvesting). Initial recruits from the seed bank are temporary post-disturbance species which achieve dominance on the site within 5 years and then begin to decline by the seventh year (Ahlgren 1979a).

The literature suggests that the dominant species of the boreal forest rarely have abundant seed bank reserves, whereas the early or mid-successional species are well represented (Isaac 1982; Pratt *et al.* 1984; Vermeer 1984; Collins 1985; Morgan and Neuenschwander 1988; Morin and Payette 1988). This is true for most habitat types in which seed banks occur. However, some research in grassland (Henderson *et al.* 1988) and tundra (Ebersole 1989) habitats reports high correlations between existing vegetation and the species represented in the seed bank, implying that the abundance is a consequence of frequent and

unpredictable disturbances. Table 3.1 summarizes the size and diversity of seed banks in three boreal forests in the northern hemisphere.

To the best of our knowledge, there have been only three seed bank studies conducted in northern Ontario (Isaac 1982; Vermeer 1984; Collins 1985). These were completed as undergraduate theses at Lakehead University in Thunder Bay. Their results support the literature which suggests that dominant species of the boreal forest of northern Ontario are not abundant in seed bank reserves, whereas early and mid-successional species are. These studies indicate that the number of viable seeds present in the seed bank depends on the age and composition of resident vegetation. The amount of viable seed in northern Ontario soils ranges from 151 to 2,157 seed/m^2 (Table 3.1). These studies were, however, limited in scope, replication, and experimental design.

Ahlgren (1979a,b,c) studied the amount of seed in the soil in northeastern Minnesota, prior to and after disturbances (harvesting and fire) to determine whether soil-stored seed is important in lands managed for timber production. In Table 3.1, Ahlgren (1979b) found almost three times as many seeds in the disturbed jack pine areas as in the undisturbed areas indicating, that much of the seed was of post-disturbance origin. His results indicate that the seed bank is an important source of seed for the initial stages of post-disturbance plant succession.

Table 3.1. Size and diversity of seed banks in several boreal forest types.

Vegetation Type	Viable Seed/m^2	Number of Species	Source
Northeastern Minnesota			
Jack pine			
Uncut & Unburned	1,016	10	Ahlgren (1979b)
Cut & Unburned	2,976	10	
Cut & Burned	2,807	7	
Red pine			
Burned	2,428	10	Ahlgren (1979c)
Unburned	392	8	
Sweden			
Scots pine			
16 yr	425	10	Granström (1982)
29 yr	240	7	
50 yr	730	10	
Spruce			
120 yr	675	7	
Pine-spruce-aspen			
169 yr	763	5	
Northwestern Ontario			
Mixedwood 55 yr	2,157	44	Isaac (1982)
Poplar 50 yr	1,880	41	
Jack pine			
9 yr	350	19	Vermeer (1984)
14 yr	368	19	
70 yr	151	12	
Mixedwood			
85 yr	1,732	16	Collins (1985)
85 yr	1,307	10	
85 yr	1,273	13	

3.2 DECIDUOUS FOREST SEED BANKS

Work on seed banks in the deciduous forest includes that of Numata *et al.* (1964), Marquis (1975), Moore and Wein (1977), Graber and Thompson (1978), Morash and Freedman (1983), Piroznikow (1983), Nakagoshi (1985), Pickett and McDonnell (1989), Dong (1990), Matlack and Good (1990), and Houle and Payette (1990, 1991). From these works, some generalisations emerge concerning deciduous forest seed banks. As in other communities and forest types, the resident seed bank does not necessarily mirror the current stand conditions, but often represents early or mid-successional species, except in large, recently disturbed gaps or abandoned fields (Numata *et al.* 1964; Moore and Wein 1977; Morash and Freedman 1983; Piroznikow 1983; Pickett and McDonnell 1989). Matlack and Good (1990) found that fire frequency and moisture availability, factors which define above ground communities, are related to the heterogeneous distribution of seeds and their incorporation into the seed bank. Morash and Freedman (1983) studied three mature hardwood forest sites and two clearcut sites and found the largest seed bank on a 5-year-old cut over. They found early- and mid-successional species were abundant in the seed bank and were well represented in the vegetation; however, the number of seeds of mature forest species in the seed bank were lower despite the predominance of such species in the stand. This suggests that the size and diversity of the soil seed bank decreases as succession proceeds. Dong (1990) intensively studied a clearcut hardwood stand in New Brunswick, and found that only the seeds if small-seeded species penetrated the litter and moved into the mineral-soil layer. After further disturbances were created by researchers in the clearcut as a result of removing the litter layer, Dong (1990) found that the disturbed sites had approximately 80% of the seed removed from the seed bank. It must be noted at this point that during some disturbances (e.g., scalping or scraping) seeds are merely displaced rather than eliminated.

The depth of a seed in the soil has been found to significantly affect its viability in all habitats (Kellman 1974; McGraw 1980, 1987; Pratt *et al.* 1984; Morin and Payette 1988). Kramer and Johnson (1987) found that most viable seed occurs within 5 cm of the soil surface. As with other types of seed banks, the number and viability of seeds decrease with increasing depth in the soil in deciduous forest types (Numata *et al.* 1964; Moore and Wein 1977; Graber and Thompson 1978; Piroznikow 1983). Soil type also has an effect on the size and type of seed banks. Factors that limit population size and diversity in seed banks include low soil pH, high organic or peat content, and low mineral-soil content (Silc and Haavisto 1970; Moore and Wein 1977; Hill and Stephens 1981; McGraw 1987). Houle and Payette (1990) found most of the seed that in an undisturbed yellow birch stand bank occured in the litter, and 99% never became successfully established. Table 3.2 summarizes the size and diversity of seed banks in seven temperate deciduous forests.

The species composition of the seed bank often relates to the species' strategies (Pickett and McDonnell 1989). Species that are described as shade-intolerant, early successional or colonizing are often the most abundant species in the seed bank of a deciduous forest (Numata *et al.* 1964; Marquis 1975; Moore and Wein 1977; Nakagoshi

1985).

Table 3.2. Size and diversity of seed banks in several deciduous forest types.

Vegetation Type	Viable Seeds/m^2	Number of Species	Source
Pennsylvania			
Yellow birch			
35 yr	370	6	Marquis (1975)
53 yr	469	7	
65 yr	617	6	
70 yr	296	6	
+100 yr	99	6	
New Hampshire			
Birch-beech-maple			
5 yr	287	38	Graber and Thompson
38 yr	1,903	17	(1977)
95 yr	1,942	12	
>200 yr	1,633	10	
New Brunswick			
Birch-beech	3,400	~5	Moore and Wein (1977)
Maple-beech	1,950	~5	
Maple clear-cut	1,390	~5	
Maple-beech clear-cut			
1988 Disturbed	141	3[1]	Dong (1990)
Control	955	18	
1989 Disturbed	16	23	
Control	247	18	
Nova Scotia			
Sugar maple 75 yr	1,096	23	Morash and Freedman
White birch-sugar maple	859		(1983)
Red maple-white birch	706		
Clear cut 5 yr	4,748		
Quebec			
Yellow birch			
Summer	828	1[2]	Houle and Payette (1990)
Fall	1,895		
New Jersey			
Oak-pine	265	46	Matlack and Good (1990)

[1] seed bank species were classified as yellow birch, raspberry and other.
[2] seeds were separated, and only yellow birch was tested for viability.

Seed banks are important factors in the regeneration of disturbed communities and ecosystems even though not all species of a successional series reside in the community (Baskin and Baskin 1978; Nakagoshi 1985; Pickett and McDonnell 1989). Species that regenerate vegetatively are very rarely found in the seed bank (Marquis 1975), whereas opportunistic species are abundant (Morgan and Neuenschwander 1988).

There has been very little research conducted on the seed banks of the deciduous forest types in northern Ontario, and this has resulted in a lack of basic information on the role seed banks play in vegetation dynamics in theses forests. Isaac (1982) and Collins (1985), however, have completed some work in boreal mixedwood seed banks (as discussed in section 3.1). Northern Ontario primarily contains extensive tracts of coniferous forest cover types, with smaller amounts of pure stands of deciduous trees. However, deciduous forest species are extremely important in the boreal forest and better knowledge of the seed banks of deciduous species is required. As illustrated in Table 3.1, Moore and Wein (1977) found that deciduous stands generally support richer and denser seed banks than coniferous stands.

3.3 OTHER TYPES OF SEED BANKS

Seed banks are found in a variety of other types of habitats, including arctic and alpine sites (Johnson 1975; Whipple 1978; McGraw 1980; Freedman *et al.* 1982; Fox 1983; Archibold 1984; Conn *et al.* 1984; Morin and Payette 1988; Ebersole 1989; McGraw and Vavrek 1989; Chambers *et al.* 1991), grasslands and fields (Rabinowitz 1981; Rice 1989; Hockley and Mayhead 1990), pastures and meadows (Keddy *et al.* 1989; McIvor and Gardener 1991), waste lands (Archibold 1980; Farmer *et al.* 1982), tropical forests (Putz 1983; Saulei and Swaine 1988; Garwood 1989), deserts (Hassan and West 1986; Henderson *et al.* 1988; Kemp 1989), wetlands (Keddy and Reznicek 1982; van der Valk 1985; Leck 1989; Wisheu and Keddy 1991), and bogs (Moore and Wien 1977; McGraw 1987).

In addition to the soil type of the seed bank, seed that remains stored in the cones or fruits of trees constitutes a canopy seed bank. Seed is held in the canopy until conditions permit dispersal, as in the case of serotinous and semi-serotinous tree species. Extensive work has been done on canopy seed banks for *Banksia* spp. in Australia (Cowling *et al.* 1987; Zammit and Westoby 1988; Enright and Lamont 1989; Lamont 1991; Lamont *et al.* 1991). It has been determined that canopy seed banks in Austrailia are of major importance to the regeneration of *Banksia* spp. and other species that are considered to be serotinous and semi-serotinous require fire or high heat intensity for their seeds to be released.

In North America, several species, including the pines and spruces, are considered to be serotinous and semi-serotinous. There is a high degree of serotiny and fire-stimulated seed release for jack pine, which retains cones with viable seed for more that 20 years (Cayford and McRae 1983). Skeates and Haavisto (1987) compiled reported seed yields of black spruce in Ontario from several studies. They summarized data on yields per tree, yields per hectalitre of cones and yields per hectare by age of trees and age of cones. With this in

mind, further research should be initiated to determine the amounts and viability of canopy-stored seed in spruces and pines, as well as the effect of fire and its intensity on the seed and its release.

4.0 SEED BANK DYNAMICS AND FOREST SUCCESSION

The dynamics of seed banks are primarily influenced by inputs to and losses from the seed bank (Parker *et al.* 1989). Factors that control these inputs and losses vary on temporal and spatial scales. Temporal factors include seed production and dispersal, habitat quality, seed germination, and environmental fluctuations. Spatial factors are principally influenced by the distribution pattern of source individuals, including: the timing of dispersal, the size of seed crop, seed quality, and gaps in suitable habitat. Differential shifts in the relative importance of seed production, predation, dispersal, dormancy, and species strategies can account for much of the observed differences between seed banks (Parker *et al.* 1989).

Environmental conditions can also affect seed bank dynamics through their influences on other habitat conditions, including: soil conditions, turnover rate, transient vs. persistent strategy, predation, and competition. Much of the work on seed bank dynamics has been to categorize and describe the amount and diversity of species which suggests that the seed bank plays an important role in succession. Succession can be defined simply as the replacement of the biota of an area by a different species (Spurr and Barnes 1980).

In nearly all published articles on seed banks and vegetation conditions, with a few notable exceptions, buried seed populations (i.e., the seed bank) for the successional series sampled did not correspond exactly to the aboveground vegetation; much of the seed bank represented an earlier stage of succession at that site. Some specific papers on the role of seed banks in succession (Numata *et al.* 1964; Donelan and Thompson 1980; Partridge 1989) suggest that the seed bank plays the most important role in establishing the initial floristic composition following a disturbance. The rapid establishment of vegetation on a disturbed site may contribute to a high degree of site stability by minimizing soil erosion and nutrient loss. The survival of seed bank germinants is critical to the recolonization of the site (Morin and Payette 1988; Ebersole 1989; Dong 1990). This initial post-disturbance establishment from the seed bank, however, may also impede the successful regeneration of desired species (Morash and Freedman 1983). Factors that affect this critical establishment period include climate, environment, and the nature and intensity of the disturbance.

The seed bank plays an important role in secondary succession of forested and non-forested sites. The nature and degree of disturbance inflicted on a site are the major determining factors in the realization of the existing potential of the seed bank (Granström 1986). After a disturbance, drastic changes in both species composition and distribution usually take place on the site. There are three main mechanisms by which plant colonization arises following a disturbance: (1) colonization from propagules stored on the site (the seed bank), (2) colonization from propagules imported to the site (seed rain), and (3) vegetative

reproduction, including sprouts, layers, rhizomes and root suckers of plants growing on the site at the time of disturbance. Granström (1986) found that colonizing populations of the first plants emerging from the seed bank were usually more successful than the later ones.

5.0 CONCLUSIONS

Seed banks play an important role in the revegetation of sites in various environments and tend to reflect the history of plant life throughout a habitat. Seed banks are distributed along both temporal and spatial scales, and indicate the successional trends and ecological importance of species within each community. By establishing the patterns of soil seed banks across a range of ecotypes, predictions can be made of the regeneration potential of the seed bank, competition potential, and the potential of the seed bank to support wildlife.

To date, very few studies have been conducted on boreal forest seed banks in northern Ontario. The existing studies were primarily undergraduate theses at Lakehead University (Isaac 1982; Vermeer 1984; Collins 1985). These studies indicated that there is a significant variation in the number of viable seeds present in the seed bank, depending on the age and composition of resident vegetation. The studies, however, were limited to one stand type, possibly with insufficient replication and inadequate experimental design. Due to the minimal number of studies that involve soil seed banks in northern Ontario, a lack of knowledge currently exists on the seed content of northern Ontario forest soils, the relationship of this seed bank to the vegetation, and the dynamics of seed banks in the boreal forest. Research must be conducted in northern Ontario to gather information on the soil seed bank across a range of forest types and to evaluate the potential of the seed bank as a mechanism of regeneration. It is important to understand the potential effects of disturbances, especially harvesting and silvicultural operations, on the distribution of seeds and seedbed types, as these control the subsequent distribution and abundance of regeneration.

The greatest test of our understanding of ecological principles is to use this knowledge to manage our forest ecosystems better. Understanding the seed bank and the processes involved within it, will increase our knowledge of post-disturbance vegetation patterns. This will then allow us to predict more accurately where and at what point vegetation from the seed bank may become a problem or a benefit. Increased knowledge of seed banks will also improve the decision-making process for the recolonization of sites, natural regeneration strategies, vegetation management and control.

6.0 RECOMMENDATIONS

The importance of soil seed banks in various types of ecosystems has been well documented. Because little is known about seed banks, revegetation, and succession after a disturbance in northwestern Ontario, we cannot completely describe and/or model the vegetation dynamics of such ecosystems. A study designed to describe the vegetation dynamics (including seed banks) of various ecosystems should be initiated and tied into the

current Forest Ecosystem Classification (FEC) system (Sims *et al.* 1989). A seed bank study initiated in northern Ontario, therefore, should be designed to:

1. quantify the seed bank in the forest soil for a variety of northern Ontario forest types,
2. determine the conditions that favour effective recruitment from the seed bank,
3. examine the process of incorporation of seeds into the seed bank.

The more specific questions this study should address include:

1. Does the seed bank represent the current aboveground vegetation or an earlier successional stage?
2. Can the seed bank correlate with post-disturbance vegetation in frequency and distribution?
3. What are the inputs and losses to the seed bank?
4. What is the timing of germination from a seed bank and the germination strategies?
5. Is the seed bank within an ecotype static or dynamic?

A seed bank study could be approached from the point of view of the species strategies. The expected seed bank should be estimated using sampling techniques that would best represent the spatial (including depth) pattern of seed distribution. The method of estimating the seed content in the soil should also be thoroughly considered to account of the advantages and disadvantages of each method. Dormancy and germination requirements should be given careful consideration when preparing samples to germinate seeds in the seed bank. In the past, a lack of consistency has led to low population and diversity estimates for seeds in the soil. Field methods should include soil and vegetation surveys so that correlations between the seed bank and the aboveground vegetation can be analyzed. Finally, as much information as possible should be gathered, for each site, on input (seed rain) to and losses from the seed bank.

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APPENDIX A: Species phenology and seed dispersal information for common seed bank species in northern Ontario.

SEED BANK SPECIES	SOURCE	SEED RIPENS	SEED DISPERSED	DISPERSAL MODE	DISPERSAL DISTANCE
TREE SPECIES					
Abies balsamea	Ahlgren (1979a,b)	Aug-Sept	Sept	wind	160 m
Betula papyrifera	Kellman (1974)	July-Sept	July-Sept	wind	91-183 m
B. alleghaniensis	Houle & Payette (1990)	Aug-Oct	Sept-Mar	wind	90-183 m
Picea glauca	Ahlgren (1979a,b)	Aug-Sept	Sept-Jan	wind	61-122 m
Populus tremuloides	Graber & Thompson (1978)	June	June	wind	many km
SHRUB SPECIES					
Cornus stolonifera	Kramer & Johnson (1987)	July-Oct	Oct-winter	bird/mammal	N/A
Diervilla lonicera	Collins (1985)	N/A	N/A	wind	N/A
Kalmia polifolia	Mallik (Pers. Comm.)	Sept-Oct	Jan-Dec	gravity	N/A
Lonicera canadensis	Ahlgren (1979a,b)	July-Aug	July	bird/mammal	N/A
Prunus virginiana	Kramer & Johnson (1987)	July-Oct	Jan-Dec	bird/mammal	N/A
Prunus pensylvanica	Ahlgren (1979a,b)	July-Sept	Jan-Dec	bird/mammal	N/A
Ribes spp.	Kramer & Johnson (1987)	Aug	Aug-Oct	bird/mammal	N/A
Rosa acicularis	Pratt *et al.* (1984)	Aug-Sept	Jan-Dec	bird/mammal	N/A
Rubus idaeus	Isaac (1982)	July-Oct	July-Oct	bird/mammal	N/A
Salix spp.	McGraw (1987)	June-July	June-July	wind/water	many km
Sambucus spp.	Graber & Thompson (1978)	June-Aug	June-Nov	bird/mammal	N/A
Vaccinium myrtilloides	Morash & Freedman (1983)	July-Aug	Aug	bird/mammal	N/A
Viburnum spp.	Rowe (1983)	July-Aug	Aug	bird/mammal	N/A
HERB/GRASS SPECIES					
Aralia nudicaulis	Morash & Freedman (1983)	Aug	Aug	bird/mammal	N/A
Aster macrophyllus	Kramer & Johnson (1987)	N/A	N/A	N/A	N/A
Cornus canadensis	Ahlgren (1979a,b)	Aug	Aug-Oct	bird/mammal	N/A
Fragaria virginiana	Kramer & Johnson (1987)	N/A	N/A	N/A	N/A
F. vesca	Kramer & Johnson (1987)	N/A	N/A	N/A	N/A
Galium triflorum	Kramer & Johnson (1987)	N/A	N/A	N/A	N/A
Calamagrostis	Conn *et al.* (1984)	N/A	N/A	wind	N/A
Carex spp.	Kellman (1974)	N/A	N/A	wind	N/A

Note: Data from Schopmeyer (1974), Sims *et al.* (1990), Bell (1991) and Walsh and Krishka (1991).

APPENDIX B: Stratification and germination requirements for common seed bank species in northern Ontario.

	STRATIFICATION				GERMINATION TEMPERATURE	
	WARM		COLD			
	TEMP (°C)	TIME (DAYS)	TEMP (°C)	TIME (DAYS)	DAY[1] (°C)	NIGHT (°C)
TREE SPECIES						
Abies balsamea	-	-	1-5	28	30	20
Betula papyrifera	-	-	1-5	30-60	32	15
B. alleghaniensis	-	-	1-5	60-75	32	15
Picea glauca	-	-	1-5	60-90	30	20
Populus tremuloides	-	-	-	-	31	28
SHRUB SPECIES						
Cornus stolonifera[2]	-	-	1-5	30-60	30	20
Lonicera canadensis	-	-	-	-	30	20
Prunus virginiana	20	60	3-5	90	25	12
P. pensylvanica	-	-	3-5	120	25	12
Ribes spp.	-	-	0	90	25	5
Rosa acicularis	-	-	1-5	120	18	18
Rubus ideaus	-	-	2	120	30	20
Salix spp.	-	-	-	-	30	20
Sambucus spp.	20-30	30-60	5	90-150	30	20
Vaccinium myrtilloides	-	-	0-3	83	-	-
Viburnum spp.	20-30	60-90	0-5	30-60	30	20
HERB SPECIES						
Aralia nudicaulis	20-30	60	5	60	30	20
Cornus canadensis	25	30-60	0	120-150	30	20

[1] based on an 8 hour daylength.
[2] soak for 1 hour in sulfuric acid.

Note: Data from Schopmeyer (1974)